

the Upper Lias in Gloucestershire, which, according to Mr. Hull of the Geological Survey, amounts at least to 200 feet in many parts of the Cotswolds.

These strata, as well as those of the Inferior Oolite, are perfectly horizontal. When the Railway was in progress, the top beds of the Lower Lias just below the Marlstone were exposed at Kilsby, and were as usual very rich in fossils, similar for the most part to those found in the equivalent strata at Campden, and Hewlett's Hill near Cheltenham.

The summit of Edge Hill in Warwickshire is capped by the Marlstone, the Upper Lias having been denuded; but small boulders of the 'fish bed,' containing scales of fish and '*Inoceramus dubius*,' are of frequent occurrence in the vale below, showing that it formerly occupied its normal position above the Marlstone in that district.

At Alderton, in Gloucestershire, the following strata were exposed below the 'fish bed' in April 1856, which seemed to be richer in fossils than usual, and therefore I have noted them here, which will enable the reader to compare them with those at Bugbrook above mentioned.

Brown and dark shales with many *Ammonites*, *Inoceramus dubius*, *Rostellaria* (abundant), *Cidaris**, *Nucula*, *Avicula*, and *Aptychus*. These are succeeded by two or three blue marly bands divided by shale, which contain a univalve like a *Cerithium*, *Avicula*, *Nucula*, *Pholadomya*, *Pecten*, *Astarte*, and *Ammonites*. A light blue, slightly indurated marl reposes immediately upon the Marlstone. The total thickness of these clays and marls forming the base of the Upper Lias is about 30 feet.

VIII.—*Contributions to the knowledge of the Anatomy of Nautilus Pompilius, L., especially with reference to the male animal.*

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[With two Plates.]

THE Cephalopod Mollusks belong to those animals in which the sexes are distinct. Long ago the anatomical investigations of Swammerdam, Monro, Cuvier and others made us acquainted

* A similar small species of *Cidaris* (*C. minuta*) occurs abundantly with spines attached in the Upper Lias shale at Gretton near Winchcomb, where a fine specimen of a *Lepidotus* was lately discovered in the 'fish bed,' and is now in the collection of my friend Dr. Wright.

† From the Transactions of the Dutch Royal Academy of Sciences, 1856. Translated by Wm. Clark, M.D., F.R.S., Professor of Anatomy in the University of Cambridge.

with the organization, and in particular with the organs of propagation of these animals. Less notice has been taken of the external sexual difference; but from the silence of writers it might be suspected that the difference in question must be on the whole not great or interesting, as indeed in some species we know with certainty that such is the case*. To this, however, besides the genus *Argonauta*, some species also of the genus *Octopus* form exceptions. In male individuals of the last-named animal one of the arms lies in a bladder, from which it is developed at the time of copulation, is detached from the body and is taken into the shell of the female, where some years ago it was several times met with, and first, under the name of *Hectocotylus* † and *Trichocephalus acetabularis* ‡, was regarded as a parasitic animal form, and afterwards as the male animal itself, before the true bearing of the matter, as we have given it in few words, was recognized §.

Ever since the animal that inhabits the shell so long known as *Nautilus Pompilius* was described by Owen ||, the principal question remained here also for investigation—what is the amount of sexual difference in this species? The individual so admirably investigated by Owen was a female, as were also those which were described after him by Valenciennes and W. Vrolik ¶. The question, how far the general structure as well as the external

* In *Loligo* the female appears to be more elongate, at least Verany states this to be the case in *Loligo vulgaris* and *Loligo sagittata*. (Mollusques méditerranéens. Gènes, 1851, 4to, pp. 99, 109.) In *Sepia officinalis*, on the other hand, the female is rounder, and the males differ in having a white stripe around the fins (*ibid.* p. 69). In *Sepiola dispar*, Krohn has observed that the female is distinguished by larger suckers (Verany, *ibid.* p. 65). Delle Chiaje states that the males remain smaller, and that, particularly in *Loligo sagittata*, the male is one-fourth shorter than the female. (Memorie sulla Storia e Notomia degli Animali senza Vertebre del Regno di Napoli. 1829, p. 97.)

† Cuvier in the *Annales des Sc. Nat.* xviii. 1829, pp. 147–156.

‡ Delle Chiaje, *Memorie sulla Storia, &c.*, ii. 1825, p. 225.

§ See on this discovery Verany, *op. cit.* pp. 126–129, pl. 41; H. Müller, Ueber das Männchen von *Argonauta Argo* und über die Hectocotylen; *Zeitschrift für wissenschaft. Zoologie*, iv. 1853, s. 1–35. tab. 1; compare Verany and Vogt, *Ann. des Sc. Nat.* 3 série, xvii. 1852, *Zool.* pp. 147–188, pl. 6–9, and R. Leuckart, Ueber die Hectocotylen von *Octopus Carenæ*; *Zool. Untersuchungen*, 3tes Heft. (Of this arm there must thus be an annual reproduction, respecting which I do not know whether any actual observations have been obtained.)

|| Memoir on the Pearly Nautilus. London, 1832, 4to.

¶ Valenciennes, *Nouvelles recherches sur le Nautilé flambé*, *Archives du Muséum*, ii. 1841, p. 257–314; W. Vrolik, Brief aan den Gouverneur-Generaal J. J. Rochussen, over het ontleedkundig zamenstel van den *Nautilus Pompilius*, in the *Tijdschrift voor de wis- en natuurkundige Wetenschappen*, uitgegeven door de Eerste Klasse van het Koninklijk Nederlandsche Instituut, ii. 1849, bl. 307–324.

form varies in the two sexes, was the more interesting, since the *Nautilus* differs in so many respects from all other cephalopods which belong to the present history of the earth, and finds its nearest affinities alone in fossil species of its own genus and of the numerous families of the Ammonites, an extinct group belonging to periods long passed away. Some years ago I happened to become possessed of a male specimen of this animal species, which however was in such a mutilated condition as to render the investigation of the internal parts impossible. Such deviations as I observed in the external parts of this specimen might still, however, be the result of occasional malformation, likely perhaps to occur in an equal degree in a female individual. In the description therefore which I gave of this specimen in the 'Instituut van Wetenschappen, Letterkunde en schoone Kunsten*,' I chose to abstain from a decided opinion, and to leave it undetermined whether there was here an individual modification of form or really a normal sexual difference. I advanced the latter as a surmise, which however appeared to be highly probable when, amongst the still increasing number of specimens brought to Europe, the same or similar deviations of form had not been observed.

From the year 1827, when I investigated this specimen, my attention was constantly directed to this point, and I am now in a condition to determine the question with full certainty. In the spring of 1855 I received, through the courtesy of his Excellency the Governor-General of the Dutch Indies, certain specimens of *Nautilus*, amongst which were several males in various states of preservation; and although all of them were thus not well adapted for the investigation of the internal organs, they nevertheless presented all the external parts uninjured, and agreed in the most minute particulars with the specimen examined in 1847.

Consequently I am no longer satisfied with a surmise, but am able to assert with perfect certainty, that in the external parts in the two sexes of *Nautilus Pompilius* a remarkable and constant difference prevails. To state clearly in what this difference con-

* 1848, bl. 67-73, pl. 1. figs. 1-3. These observations were afterwards published in the *Trans. of the Zool. Society*, vol. iv. part i. London 1851, pp. 21-29, pl. 5-8, under the title of "Contributions to the knowledge of the Animal of *Nautilus Pompilius*."

With respect to a peculiarity there announced, that in the spaces which the follicular appendages of the anterior branchial artery enclose, I had found a stony concrement, I may remark, that the same thing occurred to me afterwards in another specimen. The ossicle, investigated by Dr. L. C. Levoir at my request, weighed 0.47 grain (dried 0.438); had a spec. gr. of 1.66; it contained some traces of albumen, but no uric acid; and 70.4 per cent. of inorganic matter, principally neutral phosphate of lime.

sists, I think it better not to refer to and complete my former observations, but, with better means at my command, to describe continuously what I have observed. Some points must still remain in obscurity, where the investigation is confined to specimens preserved in spirit. It is therefore to be wished that these and other peculiarities in the anatomy of the animals may sooner or later be investigated by careful anatomists located in our colonies. I consider myself fortunate in having brought to light some additional facts in the anatomy of the Nautilus, which has been rendered by such an excellent investigator as R. Owen an object of common interest to all zoologists.

I.—*External form of the male Nautilus Pompilius, L.*

In the male and female Nautilus the general disposition of the body is the same. It consists of two principal portions, an anterior firmer and more muscular, comprising the organs of motion and of the senses, and including the horny beak, and a thin membranous sac in which the viscera are contained. This sac at its anterior part passes into a firm dermal lobe named the mantle, and opens externally under the first portion by the funnel formed of two lobes which lie upon one another*.

In the anterior portion we distinguish in the first place the *hood*. This is the name given by Owen to a membranous disk which the aperture of the shell encloses; it is higher behind, and, gradually becoming thinner forward, has the form of a cap. It is about 1 decimeter in length, and at its broadest part in the male has a breadth of from $7\frac{1}{2}$ to 9 centimeters. At the back part the hood is excised in the middle; this excision, about 4 centimeters in depth, corresponds to the turn of the shell which projects into its aperture. A longitudinal furrow on the upper

* Sometimes the right lobe of the funnel, sometimes the left, lies upon the other. This opening of the funnel below is a remarkable peculiarity, since in the other Cephalopods (the dibranchiate) the funnel forms a closed canal. I had already drawn attention to the fact, that this disposition in the tetrabranchiate Cephalopods (*Nautilus*) may be regarded as a persistent embryonal structure, since, according to Kölliker's observations, the funnel in the dibranchiate Cephalopods is, in the beginning, formed of two lateral parts which are distinct. (*Entwicklungsgeschichte der Cephalopoden von Dr. A. Kölliker. Zurich, 1843, 4to, s. 41.*)

I will here repeat the remark, in passing, that the aperture, by which, according to Owen, the mantle is perforated for the passage of the funnel (*Memoir on the Nautilus, p. 9*), has no existence. The mantle has a uniform free margin, on which the extremity of the funnel rests. I state this, because the second edition of Owen's *Lectures on the Comp. Anat. of the Invertebrated Animals*, which appeared after my 'Contributions,' still retains, by some oversight, the passage, p. 579, of the former edition: "The margin of the mantle is perforated below for the passage of the muscular expiratory and excretory tube called the funnel" (1843, p. 316).

surface divides the hood into two lateral parts; the upper surface is moreover rippled with transverse furrows, which cross, especially forwards, other finer furrows that run longitudinally; it is covered by many small scattered tubercles of unequal size, of which the largest resemble the *papillæ vallatæ* of the human tongue. Under the anterior margin of the hood is seen on each side of the middle furrow, at the distance of about a centimeter, a transverse incisure or aperture, from which a dark-grey ringed tentacle can be protruded; these tentacles retreat within the hood to about $4\frac{1}{2}$ centimeters. At each side of the hood lies the thick external integument of the head, which is divided into 18 incisures*. These incisures or slips coalesce behind and form, as it were, a cup; the undermost incisures close in over the funnel and are here connected by a thick margin excised anteriorly. Four of these slips lie more outward and backward; the rest form, as it were, a *verticillus*; on the inner surface all these slips form with the hood a connected whole, which, as an external covering, surrounds circularly the membranous oral mass in which the jaws are situated. The first slip that succeeds to the hood on each side, closes immediately upon it and forms above and forwards a border, as it were, round the hood, of the same colour and surface as itself; the remaining slips lie on the side and downwards, and are not visible in the aperture of the shell, by which they are covered at the side; they are of a paler colour and present ripples indeed, but no tubercles or papillæ. In each of the slips a ringed tentacle is contained, of the same colour as the two tentacles of the hood. These tentacles project, sometimes more, sometimes less, from the apertures of the slips, in which respect great variety prevails in different specimens; they can, however, be retracted entirely within the slips. Owen has correctly remarked that the hood is formed by the coalescence of the two uppermost slips of this encircling membranous covering of the mouth.

In these parts there is no remarkable difference from those of the females which have been examined hitherto; at least the difference does not consist in the number of the tentaculiferous slips. But it seems, on the other hand, that a variety in this respect may occur which is independent of sex; for Owen counted 19 slips on each side without the hood, in the specimen which he investigated. Eighteen however appears to be here the normal number, which I observed both in male and female specimens, and which Valenciennes found in his specimen also. But it seems to me not improbable that a sexual difference does exist in the form of the hood, and that with the same mean

* In one specimen I found on the right side only 17.

length it is about 2 centimeters narrower in females. With this also is connected a difference in the form of the shell: in male specimens it is broader and rounder at the aperture, more compressed laterally in females. The margin of the aperture of the shell also is, as it seems to me, more decidedly sinuous in the male, in the female more even.

These differences are, however, of small moment in comparison with that which the investigation of the slips situated more internally, and called by Owen *processus labiales*, presents. If we divide in *Nautilus*, whatever be its sex, the thickness of the hood mesially and then turn the external slips away from each other on each side, we find that the smooth inner skin, which covers the inside of the entire sheath, formed by these slips and the hood, gives off a fold of skin to which membranous thickenings are attached. These are divided into slips, which form cases in which retractile tentacles, similar to the external but less in size, are enclosed. Let us consider this disposition in the first place in male individuals somewhat more closely. The dermal fold, of which we have spoken, is here attached downwards with a free margin to the inside of the external circle of tentacles; the margins of attachment of the left and right sides of the dermal fold are distant from each other about 15 millimeters. Upwards on this fold is seen a membranous thickening (*labial process*) of about 3 centimeters in length, which at its anterior margin splits into eight flat digitiform sheaths. Through each of these sheaths there passes a ringed tentacle. The two uppermost slips are short, placed low on the basal part of the lamiform thickening, and are bent backwards; the six remaining slips are placed higher and are longer*. On the outside of this same dermal fold, but still also arising from it, there lies downwards, on the right side, a small membranous lobe which splits into four tentaculiferous slips. On the left side, in the same position, but extending farther backwards and more clearly distinct from the dermal fold, is found a large and thick body which is formed by the union of four largely developed and modified tentacles. We name this body, to which we shall recur, the *spadix*. It is the most characteristic part of the male *Nautilus*.

Besides these lobes and the tentacles contained in them, no other organs are found within the ring of the large tentacle-slips. The fold, so often spoken of, passes from above inwards into the skin which covers circularly the membranous, large, round, muscular mass surrounding the beak, and which, around the apex of the jaws, terminates in many short and tortuous

* The breadth on the left side amounts to 1, on the right side to 2 centimeters.

filaments, just like a border of fringe. At the commissure of the large tentaculiferous slips are found on the inside many furrows which are parallel to its excised anterior margin; whilst at the side and further back there are small cavities, from which the part obtains a retiform aspect. A continuation of the skin, at about 1 centimeter behind the excised margin, mounts upwards as a thin investment, to cover the tongue-bone, so named by Owen, and the entire muscular apparatus of the jaws, and passes into the skin arising from the dorsal surface, or rather forms a whole with it. Downwards, however, this membrane forms still another duplicature, a blind longitudinal sac, which invests a composite organ. From the transverse fissure above the duplicature, this organ comes partly into view by its superior margin. It is about 14 mm. broad and 18 mm. long, convexly oval on its upper surface, flat on its inferior surface, and lies like a little cushion below and behind the tongue-bone, and next the under surface of the commencement of the œsophagus. On opening the fold of skin that encloses it, this organ is found to consist of two lateral parts, bean-shaped, and turned towards each other at the fore-part with a convex margin. These two margins are divided by seven or more incisures* of 2 to 3 mm. in depth, into flat quadrangular slips that become narrower inwards. If the two lateral parts be separated from each other by a longitudinal section, then in each of them about fourteen other very thin laminae are seen running obliquely towards the inner margin and downwards. The most external of these laminae lies next a sinuous, smooth part, which becomes broader downwards. On the outside of this part is a small cavity within the very thick outer wall, which is formed by transverse loose fibres.

Let us now compare this disposition with what occurs in female individuals of *Nautilus*. Here there are on each side two lobes, which are divided into digitiform slips (*labial processes*, Owen). The *uppermost pair* is broader, and usually or almost always bears twelve tentacles†. The fold of skin which unites these lobes at the under side with the most external large tentaculiferous slips is covered by a number of fine membranous leaflets, which are distinguished into two groups. The *undermost pair* lies *within* the circle of the uppermost, and immediately towards the membranous mass which surrounds the jaws; they consist of a styliform part, which passes into a broader hand-shaped part forwards, and mounts at the side towards the membranous oral mass. Here I found sixteen tentacles on the

* In the specimen investigated by me in 1847, there were ten or eleven of these tetragonal slips. Trans. of Zool. Soc. iv. 1. p. 27. pl. 8. fig. 9.

† Here Owen and W. Vrolik found twelve *tentacula*, with which my observations constantly agreed; Valenciennes found thirteen.

right side, fourteen on the left side*. Within these innermost tentaculiferous slips, under the membranous mass of the mouth, there lies a part formed of eighteen or seventeen folds, which Owen considered to be the olfactory organ, but which, in my opinion, ought to be regarded as a continuation of the circle of innermost tentacles, which are here present in a rudimentary state. This part rests upon the fine membranous leaflets of the commissure of the preceding slips.

Here then it is apparent that a sexual difference exists. This difference, as to its nature, must be investigated more closely. It may be supposed that in the male Nautilus, as in the female, two pairs of labial processes are present. The first pair then would seem in the male to be placed *above* and *internally*, and to carry eight tentacles, whilst in the female it is placed *above* and *externally*, and carries twelve tentacles; the second pair would seem to differ from the undermost *processus labiales* of the female in the small number of only four *tentacula*, and still more in lying on the *outside* of the uppermost slips.

It was thus that I conceived the difference at an earlier period†. Closer investigation, however, produced a different conception, which I think preferable. Both sets of slips then in the male individual are attached to the same dermal fold, although the undermost set lies on the outside of the fold. I think, therefore, that these two groups of tentacles in the male Nautilus correspond to one pair alone of the labial slips of the female Nautilus, and that they are developed at the expense of the other pair. The commissure at the under side shows, that the pair to which they correspond is that of the outermost labial slips of the female Nautilus. In this way of conceiving the matter, the number also of the tentacles in the two sexes corresponds (8 + 4 in the male, 12 in the female).

The sexual difference may now be stated more clearly. The external labial slips are separated into two divisions, of which the undermost lies downwards and carries four tentacles. On the left side, this group of four tentacles is developed to form the *spadix*. The undermost or innermost labial slips appear to be wanting in the male. As rudimentary *processus interni* or *inferiores*, those parts however may be perhaps regarded which compose the organ at the innermost commissure, situated under the tongue and the jaws. The projecting leaflets in that part corre-

* In one specimen I found fourteen on the right side, thirteen on the left. Owen gives to these slips, as well as to the external labial slips, twelve tentacles; Valenciennes gives thirteen to each side; W. Vrolik, fourteen. Thus it appears that individual variety exists here, but that a greater number than in the external labial slips is to be regarded as the rule.

† Trans. of Zool. Soc. iv. 1. pp. 26, 27.

spond then with a greater fineness to those laminæ, which, with Owen, in his description of the female *Nautilus*, bear the name of olfactory organ. The fine membranous parts, on the other hand, which are present in the female at the commissure of the external labial slips, are entirely wanting in the male, and are represented by the retiform tissue that covers on the inside the commissure of the outermost tentaculiferous slips.

Let us now revert to the *spadix* on the left side of the male *Nautilus*. This body is 6 or 7 centimeters long, $4\frac{1}{2}$ or 5 centimeters high, and at the base 3 centimeters broad. A transverse section (Pl. V. fig. 1) plainly shows that it consists of four *tentacula*, of which three in particular are distinguished by their remarkable circumference, and of which the sheaths have mutually coalesced*. The undermost tentacle has only a short membranous sheath at its base, and elsewhere lies free along the inferior margin at the outside of the chief body of the *spadix* formed by the three remaining tentacles. On the outside of the membranous sheath of the uppermost tentacle of the *spadix* lies, close to the anterior extremity, a flat disk of an elongated round form, of $2\frac{1}{2}$ centimeters in the smaller diameter and 3 centimeters long. This disk is perforated by many small round apertures which are surrounded by a slightly raised border; they are distant from each other about 1 mm., in some places nearer together. A longitudinal section of the thickness of the disk shows that it consists of many follicles, which are perpendicular to its surface, are distinguished by sacciform dilatations of the walls, and have their openings at the apertures just mentioned.

To revert to the second principal portion of the body (p. 61), we may add, that the two swellings which are present in the undermost part of this portion in the female, are absent in the male†. The glandular organ, composed of many laminæ, which is here attached to the inside of the mantle in the female *Nautilus*, is wanting in the male; consequently Owen's opinion is confirmed, which regards this organ as connected with the sexual apparatus, and ascribes to it the secretion of a covering for the eggs‡. Moreover, it seemed to me that the mantle in the male *Nautilus* is shorter and leaves the eyes almost uncovered, whilst in female

* These tentacles present to the naked eye a structure corresponding to that which in the ordinary tentacles is observed by means of the microscope. Comp. R. Owen, On the structure and homology of the cephalic tentacles in the Pearly *Nautilus*, *Annals and Mag. of Nat. Hist.* xi. 1843, p. 308.

† Owen, *Memoir*, p. 9. pl. 1 e, pl. 2 e; compare my figures, *Transact. of the Zool. Soc.* iv. 1. pl. 5 h, pl. 6. fig. 3 h h.

‡ "A glandular apparatus . . . which, if not peculiar to, is in all probability more strongly developed in the female than in the male *Nautilus Pompilius*," p. 9. See further the description of this part, *ibid.* p. 43.

specimens the margin of the mantle extends over the middle of the anterior surface of the pedunculated eye-ball.

II.—*Male organs of propagation of the Nautilus.*

If the mantle be reflected or removed and the *Nautilus* be examined on the inferior surface, then it is found that the animal has a space or cavity which is distinct from the visceral cavity and contains the four gills. The position of the parts which are visible in this gill-sac agrees on the whole in the male *Nautilus* with that of the corresponding parts in the female. The penis however does not lie, at least not exactly, on our left hand, as does the aperture of the oviduct or the *vulva* in the female*, but almost exactly in the mid-line, between the *anus* and the funnel. This penis is of an obtusely conical form; on the dorsal surface, almost as far as its extremity, it is congruous with the skin, which is distended between two large muscular columns (the large shell-muscles), and by which the intestinal cavity is separated from the gill-sac. On our left hand, that is on the right side of the animal, is seen, between the *anus* and the first gill, at the base of the penis, a convex swelling, which is caused by a bladder lying under it.

Let us regard, however, before further consideration of the external parts, the internal organs of propagation. These consist principally of two glands, both of remarkable size (Pl. V. fig. 2). If we open on the dorsal surface the sac containing the viscera, then we find at the posterior end of this sac, on the left of the muscular stomach, the larger of these two glands, which however is in great measure concealed by the lobes of the liver, and on the right side also, in some degree, by the stomach. This gland, which, from the analogy of the other Cephalopods, must be regarded as the *testis*†, is included in a thin white membrane, as also the rest of the viscera are separately included in a similar investment. This gland has a length of about 7 centimeters, and at its broadest part a breadth of 4 centimeters; it surpasses all the rest of the viscera, the large liver alone excepted, in bulk, and with its anterior margin extends as far as the heart, thus occupying nearly the entire length of the visceral sac. It has a flat, oval form and is bounded on the left or outer side by a

* That is, on the right side of the animal, which in this position turns its back from us. See my fig., *Trans. of the Zool. Soc. l.c.* pl. 7. fig. 4.

† In the same situation in which the testis lies in the male *Nautilus*, the ovarium of the female is placed. Owen, indeed, says that the muscular stomach at the bottom of the visceral sac lies on the left, and the ovarium on the right (*Memoir*, p. 26, § 4); but this refers to the position in which the animal is figured by him (pl. 5), namely lying on its back and seen from the ventral surface.

margin convexly prominent, especially at the upper part. If the thin but strong integument of this part be removed, then the testis presents a brownish-yellow colour, and is seen to be divided into an upper and a lower half, and by transverse furrows that run obliquely into some loosely connected lobes. It is composed of a quantity of *acini*, which, with their blind extremities on the surface, look like white spots. The proper composition of the tissue of these *acini* was not apparent; the microscope indicated nothing but a granular mass. On the inside of the *testis* white ducts are seen which meet in a tube (*vas efferens*) that runs at the right side. This tube leaves the tissue of the testis, runs for a short space within the tegumentary sac, and terminates on a flat conical prominence by a small oblique aperture. The margin of this papilla presents radiating folds, and is in close union with the covering of the testis, which is perforated by the aforesaid aperture.

Above, and on the right side of the testis is situated a second gland, of a flat form, longitudinally round and smaller than the first*. It consists in part of many small lobules attached to flattish transverse partitions, and formed of microscopic finger-shaped blind tubules whose walls consist of cylindrical or conical cells (*cylinder-epithelium*). In the anterior extremity of this second sexual gland a saccule placed transversely is included, and is surrounded below by its tissue (Pl. VI. fig. 2). Behind this saccule is seen a milk-white body, in which I afterwards recognized, from the observation of Dr. J. A. Bogaard, Prosector of the Leyden University, who investigated the sexual organs of *Nautilus* with me, the convolution of a tube. I succeeded in following the course of this tube further, which was somewhat difficult, since it is in close connexion with the tissue of the gland, and for the most part is concealed in the innermost portion of it. At its anterior extremity this tube terminates between the two slips of a nipple at the right side of the above-named saccule, then follows a course to the left towards the posterior margin of the saccule, then makes marked convolutions directed downwards and upwards and lying close together, afterwards proceeds, close along the right margin of the gland, backwards, again penetrates more into its depth, and finally ends as a fine canal of about $\frac{1}{2}$ millim. in diameter. The aperture of this fine canal, scarcely visible to the naked eye, is situated on the left side of the gland, which there presents a longitudinal furrow opposite to the conical excrescence in which the *vas efferens* of

* It now appears that it was this second gland which, in the imperfect specimen described by me in 1847, I saw in front of the testis ("a round mass that fell from the visceral cavity." Tijdschr. uitgeg. door de eerste klasse van het Kon. Nederl. Instituut, i. bl. 72).

the *testis* opens. By this furrow the said conical extremity is received in the natural position of the parts, and at its bottom is a fissure which leads to a small cavity of the gland, which is covered by a membrane with slight longitudinal folds, but in other respects smooth. At the upper part in this space the fine extremity of the convoluted canal opens. This canal is thus the *deferent vessel* (*vas deferens*), and the second gland is therefore to be regarded in part as an investiture of this deferent vessel. But this vessel is also the efferent duct of the secretion effected by the glandular tissue through which it runs, and is doubtless also itself moreover the seat of a secretion, since its walls present the same cylinder-epithelium as the *acini* of the surrounding gland. These walls are very thick, especially in the upper part, so that the inner space bears no proportion to the external circumference. This, on an average, has a diameter of two millimeters: anteriorly the tube becomes wider, but not uniformly; the two principal dilatations which it presents are fully three millimeters in diameter.

The saccule, of which we spoke above, forms a *diverticulum* terminating cæcally on the left side. Its inner surface has on the right side many projecting transverse folds, and presents here a second small aperture, situated immediately above the termination of the *vas deferens*; around this aperture the said folds form some circles. It is the inferior extremity of a tube 4 or 5 millimeters in length, with a circumference of about 3 millimeters. This tube has very thick walls, and presents longitudinal folds on its inner surface. It leads to the *spermophoresac**, a cylindrical bladder with very firm walls, so that when quite empty it does not collapse. The internal cavity of the bladder has numerous projecting folds that run longitudinally, and is divided by a partition running obliquely and having a free anterior margin into two cavities which communicate at the upper part. This bladder passes immediately into the canal of the *penis* (the *urethra seminalis*), which also presents strongly projecting longitudinal folds. The thick walls of this canal, which form the *penis*, consist of a very firm tissue; on the cut surface some round apertures are visible, which appear to be the sections of blood-vessels. At the extremity of the *penis* the termination of the *urethra seminalis* is seen as a transverse aperture surrounded by a thick margin, which is divided by incisures into some tubercles; on the surface that faces downwards, in particular, two such tubercles may be obviously distinguished.

In a specimen investigated by me, which had died during the

* The French writers on the anatomy of the Cephalopods name this part *poche Needhamienne*, after Needham, who is usually regarded as the discoverer of the spermophores.

period of sexual orgasm, I found the spermophore-sac, forcibly distended by its contents, to occupy the entire space between the anus and the base of the penis near the right anterior gill, whilst a spermophore filled the penis and came partially into view at its aperture (Pl. VI. fig. 1).

The parts found by me in *Nautilus* present on the whole the same type which we remark in the male sexual organs of the dibranchiate Cephalopods. The canal which I have indicated as *vas deferens* corresponds at its uppermost wider part, furnished with thick walls, with the part that Cuvier designates as *vesicula seminalis* in *Octopus*. The saccule in which this canal terminates may be compared with the part which this illustrious anatomist and others after him have regarded as a *prostata*, although with greater justice it may be taken for a *vesicula seminalis*. The glandular tissue which surrounds and covers the *vas deferens* seems to be wanting in the rest of the Cephalopods. In the smallness of the spermophore-sac, and in some other particulars, *Octopus* approaches nearer to *Nautilus* than do *Sepia* and *Loligo*; in the *spermophores* also, a closer affinity of *Nautilus* with *Octopus* may be remarked than with the ten-armed Cephalopods.

In the upper end of the efferent tube (that part which corresponds to the *vesicula spermatica* of authors), I found spermophores still imperfect and very soft; they were more developed in the small saccule in which the tube terminates; but a greater firmness and a definite convolution in spiral turns are seen first in the sac in which they are collected under the penis.

From this Needhamian sac, which beyond doubt is contractile, the spermophores are brought into the canal of the *penis* and from thence into the gill-sac. From thence they arrive, whether through the funnel or along the free margin of the mantle, at the different parts above, which as tentaculiferous slips surround the muscular bulb of the mouth.

That the spermophores tarry there for a time, before they leave the aperture of the shell to reach the shell of the female *Nautilus*, appears to me most likely. In three specimens I have found them there, and in all at the same part. This was on the dorsal surface, under the hood, and between the two first and smaller tentacles of the two *processus labiales*, those of the left side surrounding them like two fingers, whilst a cavity was, as it were, impressed for them at the base of the right tentaculiferous lobe by a bladder which enclosed the spermophore. *For here the spermophores do not lie uncovered; on the contrary, they are enclosed in a round, brown vesicle, which is about 18 millimeters long and 15 mm. broad, and of which the walls consist of three or four structureless membranes lying upon one another.*

I consider this covering of the spermophore as one of the most remarkable peculiarities which the investigation of the male Nautilus has revealed to me. The enclosing of the spermophores in the bladder must of necessity have occurred after they had passed through the penis. Even if I had not actually met with spermophores in the canal of the penis, as stated above (p. 70), which were not yet included in such a bladder, still the considerable size of the bladder would have precluded the possibility of a passage through that canal. The membranes of this bladder are thus secreted on the outside of the visceral cavity. Where and by what organs is the secretion effected? To this question I can only answer by conjecture. In the branchial sac nothing is seen that can perform the secretion. But on the other principal portion of the body are two organs which may be noticed here. In the first place, it may be supposed that the numerous folds of the organ situated behind the lower jaw below the œsophagus (p. 64) serve for secreting. In the second place, the round glandular disk deserves consideration, which is situated on the outer surface of the *spadix*. Whilst it is uncertain whether the first-named organ discharges a secreting office, there can be no doubt respecting such a function in the second; but it does not follow from this that the secretion which occurs in the said disk is exactly for the formation of the bladder which encloses the spermophore. Had I been fortunate enough to encounter in any specimen spermophores on the road from the branchial sac to the dorsal surface of the animal, then this matter might have been susceptible of a more accurate determination.

I am not in a condition to show how the bladder with spermophores is expelled from the shell of the male at a later period. A real copulation cannot take place: not only is the penis situated too deeply in the mantle for this, and too short, but moreover the enveloping of the spermophores shows that the expulsion of the sperma by the penis has preceded by some time the impregnation. I think I cannot be wrong in regarding the enclosing of the spermophores as a means of preserving the sperma for a time from the effect of sea-water until it has arrived at the place of its destination, the branchial sac of the female Nautilus.

We will, in conclusion, treat of the structure of the spermaphores* or spermophores, as far as they can be investigated in specimens which have been long kept in spirit. It is well known that the sperma of Cephalopods is enclosed in singular bodies of very large size, which Swammerdam first described in *Sepia officinalis* as "witte en teere pennekens, die zich in water bewegen en

* Duvernoy changed this name into spermaphores: by a slight modification, after the remark of a celebrated Hellenist, we prefer to write spermophores.

openbarsten"—white and delicate tubes which moved in water and burst open*, and which Needham investigated more closely in *Loligo*, whence they afterwards obtained the name of *corpora Needhamiana*. I always found in the bladder under the hood, described above, a single spermophore alone, and have no reason to conclude that it may contain two of them. This spermophore is of an extraordinary length, and lies in the bladder rolled up in many convolutions, just as the spermophores are already convoluted in the *vesicula seminalis*. I succeeded in unrolling one of them, but not without some pieces breaking off, and thus I can estimate the length at full 27 centimeters. Dr. Bogaard estimates the length of another spermophore, measured by him, at 34 centimeters. This remarkable length is not altogether without example in other Cephalopods: Milne-Edwards found the spermophores in *Octopus vulgaris* 8 centimeters long †, and R. Leuckart found in *Octopus Carenæ* the spermophore 3 feet long (Zoologische Untersuchungen, Drittes Heft, Giessen 1854, 4to, s. 98. not. 2). The spermophore of the Nautilus is a round tube, not everywhere of the same thickness; it is on an average 1 mm., and becomes fine at the two extremities. The smaller end presents a small bending back at an acute angle; this thin recurved part is about 3 mm. long. The point, finally, presented in one specimen a microscopic appendage in addition, which seemed to be split into two slips and left the before-named thin part at a right angle.

The colour of the spermophore, when it has left the penis, is brown-yellow. Within its cavity there lies a ribbon-shaped filament of about $\frac{1}{20}$ mm. in breadth, which is visible to the naked eye. This filament is flat and bent spirally in close circles, like the spiral thread in the air-tubes of insects. It consists in great part of spermatozoids which are attached by their capilliform extremities to the structureless thread situated in the middle ‡. For other particulars I refer my readers to the careful investigations of Dr. Bogaard appended to this memoir, and put aside my own observations, which were not complete, rather than by a difference of conception give occasion, perhaps, in the reader, to uncertain and confused notions.

The structure of the *corpora Needhamiana* in the Cuttle-fish (*Sepia officinalis*) has been described exactly by C. G. Carus, who, however, has drawn up his description under the impression of a mistaken idea, that he had an animal existence

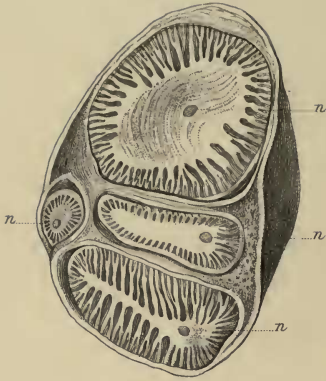
* Biblia Naturæ, p. 896.

† Ann. des Sc. Nat., 2 série, tom. xviii. 1842, Zool. p. 339. pl. 14. fig. 1.

‡ What I formerly described as flat, elongate-oval, microscopic bodies, hanging by the filament (Tijdschr. van de Eerste Kl. van het Koninkl. Instituut, i. bl. 72), I now regard as tissue detached from the spiral filament.



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